

# Phocoenoides dalli.

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## Phocoenoides Andrews, 1911

*Phocoenoides* Andrews, 1911:31. Type species *Phocoenoides truei* Andrews, 1911, by original designation.

**CONTEXT AND CONTENT.** Order Cetacea, Suborder Odontoceti, Family Phocoenidae. The family contains four extant genera: *Phocoena*, *Australophocaena*, *Neophocaena*, and *Phocoenoides* (Barnes, 1985). Barnes (1984, 1985) has proposed two subfamilies within the Phocoenidae. These are Phocoeninae; and Phocoenoidinae, which contains *Phocoenoides*. The genus *Phocoenoides* includes only *P. dalli*, with no subspecies. There appear to be two commonly-occurring color morphs.

## Phocoenoides dalli (True, 1885)

### Dall's Porpoise

*Phocaena dalli* True, 1885:95. Type locality "strait west of Adakh (Adak) Island, [in the Aleutian chain of Alaska]."

*Phocoenoides dalli* Andrews, 1911:31. Renaming of *Phocaena dalli*.

*Phocoenoides truei* Andrews, 1911:32. Type locality "Aikawahama, Rikuzen Province, Japan."

**CONTEXT AND CONTENT.** Context noted in generic summary above.

**DIAGNOSIS.** The skull (Fig. 1) is characterized by "very complex fossae and bony struts in the squamosal, basisphenoid, basioccipital and orbitosphenoid bones" (Barnes, 1985:153). The condylobasal length of adults is 309 to 339 mm, or 17 to 18% of the total length (Tomilin, 1967). The closely related spectacled porpoise (*Australophocaena dioptrica*) has a condylobasal length of 283 to 315 mm (Brownell, 1975). The rostrum is relatively broad, flat, and short, representing about 41 to 43% of the condylobasal length in *P. dalli* (Nishiwaki, 1972; Tomilin, 1967). The length/breadth ratio of the skull is 2.1, and that of the rostrum is 1.5 (Nishiwaki, 1963, 1972). The dental formula is 23 to 28 upper, and 24 to 28 lower (Nishiwaki, 1972). *Phocoenoides* can be distinguished from *A. dioptrica*, in which the dental formula is 18 to 23 upper, and 16 to 19 lower (Brownell, 1975).

There are 92 to 98 vertebrae, and the formula is 7 cervical, 15 to 18 thoracic, 24 to 27 lumbar, and 44 to 49 caudal (Nishiwaki, 1963, 1972; Tomilin, 1967). *Australophocaena dioptrica* has only 66 to 70 vertebrae (Brownell, 1975). All seven cervical vertebrae are fused in *P. dalli*. Usually there are 30 to 35 chevrons (Benson and Groody, 1942; Cowan, 1944). The vertebrae have compressed centra, and elongated dorsal and transverse processes (Miller, 1930). The ribs also are relatively long and slender (Miller, 1930). There are usually 12 pairs of two-headed, and six pairs of single-headed ribs (Nishiwaki, 1972). The phalangeal formula is: I, 1 to 2; II, 6 to 7; III, 4 to 6; IV, 1 to 3, and V, 0 to 2 (Nishiwaki, 1963, 1972).

**GENERAL CHARACTERS.** Dall's porpoises are mostly black, with a white flank patch that is continuous ventrally (Leatherwood et al., 1982). The flank patch extends about half-way up the sides and back to just posterior to the anus. A black extension surrounds the urogenital area, and usually another black line includes the umbilicus. White to light-gray areas are present on the upper half of the dorsal fin, and on the rear border of both surfaces of the flukes. Light-colored areas are also sometimes found on the peduncle, flippers, head, and throat. Black flecking is common on many of the white areas (Norris and Prescott, 1961).

There are two normal color patterns (Fig. 2): *truei*-type, which is the normal color pattern for the population off the Pacific coast of Japan; and *dalli*-type, which is the normal pattern for all other populations (Kasuya, 1978, 1982). The only demonstrable difference

between these two is in the forward extent of the white flank patch (Houck, 1976). It extends anterior to the level of the flipper in *truei*-type, and only to about the level of the anterior insertion of the dorsal fin in *dalli*-type. In addition, three other uncommonly-occurring types have been described. Gray animals resembling harbor porpoises (*Phocoena phocoena*) have been reported from Monterey Bay, California (Morejohn et al., 1973), and from Prince William Sound, Alaska (Hall, 1981). Entirely black individuals have occurred mostly in the waters of Japan (Kasuya, 1978; Nishiwaki, 1966; Wilke et al., 1953), but also from Monterey Bay (Morejohn, 1979), and from the northwestern North Pacific (Newby, 1982). Completely white animals have been observed off Japan and off Washington State (Joyce et al., 1982). Forms intermediate between *dalli*- and *truei*-types also have been examined (Houck, 1976).

Dall's porpoise is a thick-bodied animal, reaching a maximum size of 220 cm and about 200 kg (Leatherwood et al., 1982). The body shape of this species is unique. Overall it is powerfully built, and the head is proportionately small. There is little or no beak, and when present it is poorly defined. The lower jaw protrudes slightly beyond the upper jaw. The flippers are located far forward near the head, and are slightly rounded at the tips. They are small and represent about 8 to 9% of the total length (Tomilin, 1967). The dorsal fin is wide-based and triangular, with a more or less straight trailing edge. It ranges from about 6 to 9% of the total length (Tomilin, 1967). The caudal peduncle is deeply keeled, and the dorsal aspect slopes steeply to the flukes. The flukes are small, about 20% of the body length (Nishiwaki, 1972). The posterior border is usually straight, but ranges from slightly concave to convex. A shallow to moderately deep median notch is present (Leatherwood et al., 1982).

Newborn Dall's porpoises have a muted color pattern of dark-gray and light-gray tones, which intensifies to black and white in the adult (Kasuya, 1982; Morejohn, 1979). The white or light-gray frosting on the flukes and dorsal fin also develops with age (Mizue and Yoshida, 1965; Morejohn, 1979). The head of newborns is relatively large, and as the porpoise ages, the abdomen grows at a faster rate than the head (Koga, 1969; Mizue and Yoshida, 1965). Growth during the first year is rapid, after which the growth curve begins to level off (Kasuya, 1978; Newby, 1982).

There appears to be some sexual dimorphism in the black coloration that surrounds the urogenital area (Morejohn et al., 1973), although this, like most other aspects of the pattern, is highly variable. Males tend to be longer and heavier than females, and Morejohn and his colleagues (Morejohn 1979; Morejohn, et al., 1973) have found slight size dimorphism in some standard measurements. The most important of these is that the genital and anal openings are more widely separated in males than in females. The deepening of the caudal peduncle reaches its greatest extent in adult males (Houck, 1976), and males often appear to have an enlarged hump on the back between the blowhole and the dorsal fin (Newby, 1982).

**DISTRIBUTION.** *Phocoenoides* is found only in the North Pacific area (Fig. 3). When water temperatures are exceptionally cool, Dall's porpoises are found as far south as 28°N, off the coast of Baja California, Mexico; but they only occur commonly south to about 32°N in the eastern North Pacific (Morejohn, 1979). In the central Pacific, the southern limit in pelagic waters is about 41°N (Kasuya and Jones, 1984). At the northern end of the range, sightings are infrequent north of 62°N in the Bering Sea (Nishiwaki, 1967), but there have been occasional sightings as far north as the Chukchi Sea (Sleptsov, 1961). On the east coast of Japan, *P. dalli* is found south to about 35°N (Kasuya, 1978, 1982). Off the west coast of Japan, the Kurile Islands, and the Kamchatka Peninsula, a separate population is widely distributed in the Sea of Japan and southern Okhotsk Sea, but specific limits are not available (Kasuya, 1982; Okada and Hayashi, 1951; Sleptsov, 1961).

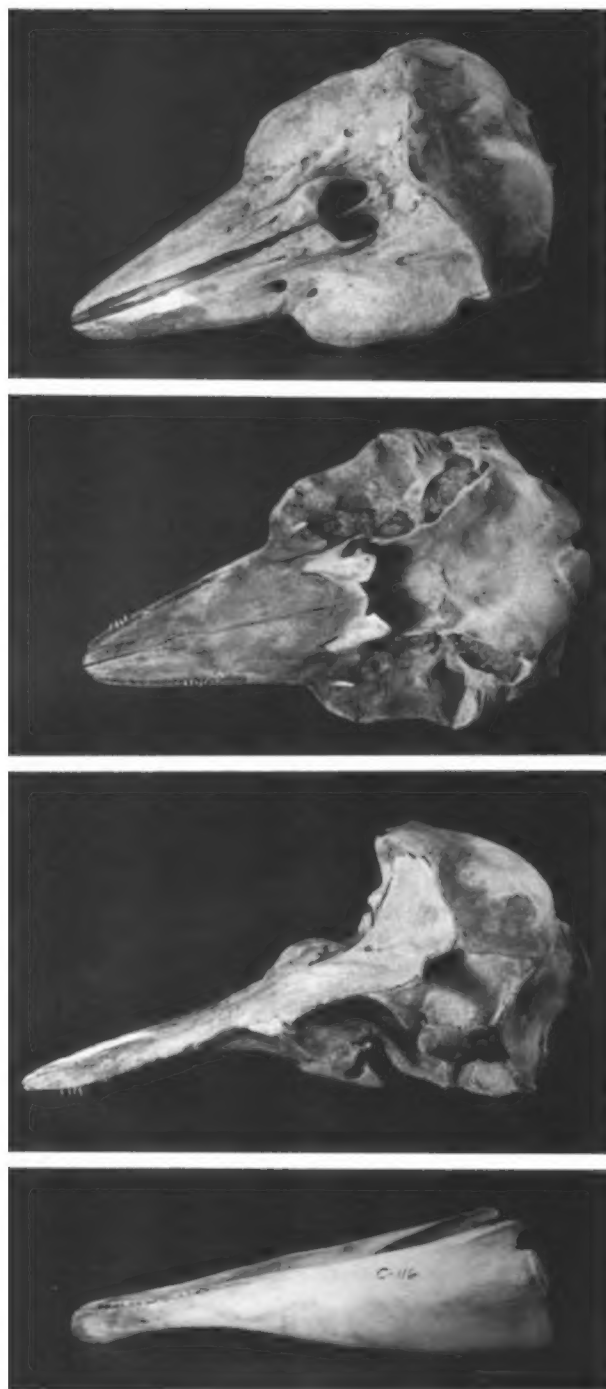


FIG. 1. Skull of *Phocoenoides dalli* (San Jose State Univ. C-116). Dorsal, ventral, and lateral views of the cranium, and lateral view of the mandible. The zygomatic arches are broken-off, and most of the teeth are missing. Greatest length of the skull is 325 mm.

**FOSSIL RECORD.** There is no fossil record for *P. dalli*. The family Phocoenidae is known as far back as the late Miocene (about 10 to 11 million years ago), from the extinct *Loxolithax stocktoni* (Barnes, 1976, 1984).

**FORM AND FUNCTION.** Turnover of skin appears to be very rapid in *Phocoenoides*. In fact, captive Dall's porpoises developed layers of sloughed skin, probably due to their inability to swim rapidly in the tank (Ridgway, 1966; Wood, 1973). Compared to other small cetaceans, Dall's porpoises tend to have a relatively thin blubber layer (Ridgway, 1966). Dermal ridges in the gums, called "gum teeth" by Miller (1929), lie between the rudimentary



FIG. 2. Lateral views of *dalli*-type (top) and *truei*-type (bottom) Dall's porpoises. *Dalli*-type is a 177 cm adult female (National Marine Mammal Laboratory TAJ 152), and *truei*-type is a 179 cm adult female (NMML TAJ 029). Both specimens were incidentally caught in gillnets in the northwestern North Pacific.

true teeth. These, along with a "dental pad" at the tip of the upper jaw, appear to function in capture of soft-bodied prey (Morejohn, 1979).

The poorly-rooted spatulate teeth of *P. dalli* apparently are the smallest among dolphins and porpoises (Morejohn, 1979). The skull, as in most other odontocetes, is asymmetrical, with the nares displaced to the left, and the left naris larger (Cowan, 1944). The tympanoperiotic bones (Fig. 4) resemble those of *Phocoena* (Kasuya, 1973). The alveoli of both the mandible and maxilla are shallow and incomplete (Cowan, 1944). The skeletal musculature of this species is large, and the lumbar muscles are massive (Ridgway, 1966).

Morejohn (1979) found the heart of *Phocoenoides* to be relatively larger than in the small delphinids *Stenella* and *Delphinus*. Ridgway and Johnston (1966) reported that the heart of this species is also larger than in *Tursiops* or *Lagenorhynchus*, but Morejohn (1979) contested this. The oxygen-carrying capacity of the blood is much higher than in other small odontocetes (Ridgway and Johnston, 1966; Ridgway et al., 1970). Compared to other species, the electrophoretic mobility of the hemoglobin is low for *P. dalli* (De Monte and Pilleri, 1969; Horvath et al., 1968). Ridgway (1972) reported marked bradycardia during experimental dives. All of these findings are likely related to the fast-swimming and deep-diving habits of Dall's porpoise.

The brain of Dall's porpoise is relatively smaller than that of most other small odontocetes (Morejohn, 1979; Ridgway, 1966). Pilleri and Gehr (1970) reported brain mass for seven animals ranging from 715 to 1,045 g (1.0 to 1.2% of body mass). The brain mass/spinal cord mass ratio is lower for *P. dalli* than for *Tursiops* or *Lagenorhynchus*, and Ridgway et al. (1966) suggested this may indicate a lower intelligence level. Bauer et al. (1985) reported the presence of magnetic material in the brain and other tissues of *P. dalli*, suggesting the possibility of magnetic navigational abilities. The external auditory canal penetrates through the blubber, but not always through the epidermis (Norris and Prescott, 1961). McCormick (1969) reported that 10 captive Dall's porpoises had never been observed to engage in any activity resembling sleep (which he identified in other species of dolphins).

This species is unique in having a fatty pad lining each lung, the function of which is unknown (Ridgway, 1966; Simpson and Gardener, 1972). The cartilaginous rings lining the trachea are thick (Ridgway, 1966). *Phocoenoides*, like other phocoenids, has vestibular air sacs which are different from those of delphinids. They are much larger, and are deeply folded, with the folds being composed of thickened connective tissue (Mead, 1975; Ridgway, 1966). The normal respiratory rate in captivity is 2 to 3 breaths/min (Ridgway, 1965).

As in other cetaceans, the stomach consists of three chambers. The liver is relatively larger than in *Stenella* or *Delphinus* (Morejohn, 1979).

The kidneys are lobulated, like those of other cetaceans (Gehr and Kraus, 1970). The normal color of the feces is gray to bright

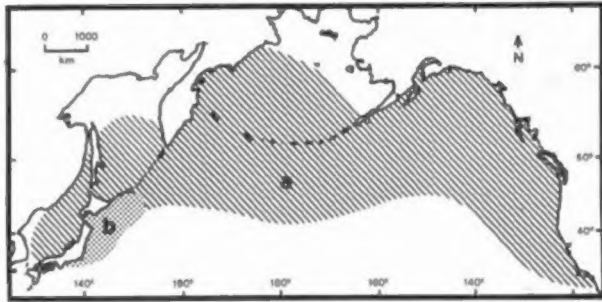


FIG. 3. Approximate distribution of *Phocoenoides dalli* in the North Pacific area: range of *dalli*-type (a), and area of overlap of *truei*-type (b; adapted from Morejohn, 1979).

green (Ridgway, 1965). Morejohn and Baltz (1972) found the reproductive tract of female Dall's porpoises to be unique in having a vaginal band (hymen), and in lacking folds in the walls of the posterior vaginal vestibule of immatures. These folds are present in adult female Dall's porpoises, as in other cetaceans.

The adrenals and the thyroid are relatively large in this species (Ridgway, 1966; Ridgway et al., 1970). Temte and Spielvogel (1985) showed a relationship between corpus luteum diameter and serum progesterone level in incidentally killed Dall's porpoises. Morejohn (1979) noted one specimen to possess a pre-anal gland pit 40 mm anterior to the anus, possibly used in chemical communication.

**ONTOGENY AND REPRODUCTION.** In recent years, knowledge of the life history and reproduction of Dall's porpoise has greatly improved. Apparently, most ovulations occur in the left ovary (Mizue and Yoshida, 1965; Mizue et al., 1966; Ohsumi, 1964), and most fetuses develop in the left uterine horn. Delayed implantation may occur (Newby, 1982).

Gestation lasts <1 year, and estimates range from 7 to 9 months (Okada and Hayashi, 1951) to 11.4 months (Kasuya, 1978). The fetal-growth rate was calculated by Kasuya (1978) to be 3.3 mm/day, and Okada and Hayashi (1951) described changes in the morphology of the fetus. Length at birth is 95 to 100 cm (Kasuya, 1978; Mizue et al., 1966; Newby, 1982).

One calf is born. Calving takes place mainly in the warmer months throughout the range. The calving peak is in late August for the Japanese-coastal population (Kasuya, 1978), and in late June to early July for the populations in the western North Pacific (L. L. Jones, in litt.), and in the Sea of Japan and Okhotsk Sea (Okada and Hayashi, 1951). Kasuya and Ogi (1987) suggested that the Bering Sea contains a separate breeding stock, and that breeding there occurs somewhat later. In the eastern North Pacific, Morejohn (1979) suggested year-round calving, but other evidence indicates a spring to summer calving peak, or possibly two peaks (Hall, 1981; Loeb, 1972; Ridgway and Green, 1967).

Kasuya (1978) suggested that Dall's porpoise calves are weaned at an age of 1 to 2 years. Loeb (1972) suggested that weaning occurs much earlier, at about 3 months. Recent evidence presented by Newby (1982) indicates that Kasuya's values may have been overestimates, and that the length of lactation may be short (1.6 to 4 months).

Males in the population located in the northwestern North Pacific and Bering Sea reach puberty at about 182 cm and 5 to 6 years (Newby, 1982). Off the Pacific coast of Japan, the estimates are 196 cm and 8 years (Kasuya, 1978). Sexual maturity of males is more dependent on length than on age (Kasuya and Shiraga, 1985). Sexual maturity of females occurs at an average age of 3 years and length of 170 to 171 cm in the northwestern North Pacific and Bering Sea (Newby, 1982), and 7 years and 187 cm in Japanese-coastal waters (Kasuya, 1978). The differences between these two populations are considered to be real, and not simply artifacts of different research techniques (Kasuya and Shiraga, 1985).

Most females in the western North Pacific and Bering Sea apparently have an annual reproductive cycle (Kasuya and Jones, 1984; Newby, 1982). Kasuya (1978) found a mean calving interval of 3 years for the Japanese-coastal population. Ovulation probably occurs within about 1 month after parturition (Kasuya and Jones, 1984).

Dall's porpoises appear to be short-lived. Kasuya (1978) found few adults in his sample from the Japanese-harpoon fishery, but

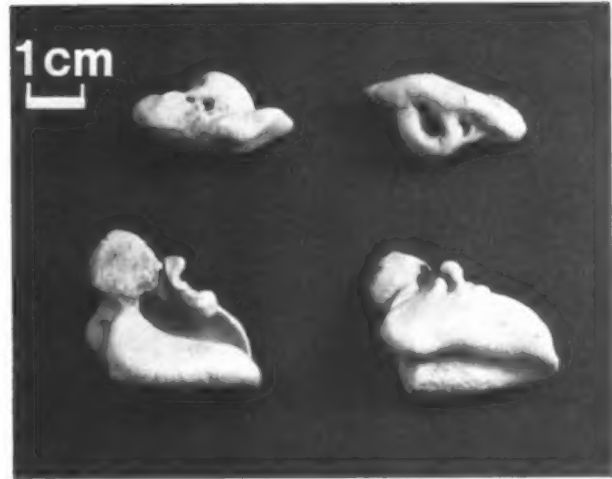


FIG. 4. Tympanoperiotic bones of *Phocoenoides dalli* (SJSU C-116): ventral view of left periotic (upper left), dorsal view of right periotic (upper right), dorsal view of left tympanic bulla (lower left), and ventral view of right tympanic bulla (lower right).

believed that older individuals were underrepresented, since they do not ride bow waves as often. The maximum age attained by animals in the northwestern North Pacific is 22 years, although most animals sampled were less than 10 years old (Newby, 1982). Annual natural mortality rates for Dall's porpoises have been estimated at 13 to 14% (Newby, 1982; Ohsumi, 1979).

Dall's porpoises are aged by counting growth layers in the cementum of the teeth, which are thought to be deposited annually (Kasuya, 1978; Perrin and Myrick, 1980). Perrin and Myrick (1980) concluded that counting of dentinal layers does not represent a reliable method of age determination for *P. dalli*. Ogden et al. (1981) described roentgenographic indicators of skeletal maturity in Dall's porpoise, but currently these cannot be used to determine chronologic age.

**ECOLOGY.** Killer whales (*Orcinus orca*) prey on Dall's porpoises (Barr and Barr, 1972; Morejohn, 1979; Nishiwaki and Handa, 1958). At other times, the two species have been seen interacting peacefully (Jacobsen, 1986; Jefferson, 1987; Scheffer, 1949). Leatherwood et al. (1982) suggested that sharks may attack Dall's porpoises, and Newby (1982) reported a possible shark wound on a porpoise. Morejohn (1979) believed that these animals can swim fast enough to avoid shark predation.

Dall's porpoises occasionally are seen in the presence of other marine mammals, most commonly Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Leatherwood et al., 1982). They also are sometimes observed swimming around large whales (Morejohn, 1979).

Dall's porpoises often are heavily infested with parasites. Walker (1975) found *P. dalli* to be the most heavily parasitized small cetacean in the southern California live-capture fishery. Common parasites of the lungs include the nematodes *Halocercus dalli* (Conlogue et al., 1985; Machida, 1974), and *Stenurus minor* (Johnston and Ridgway, 1969; Walker, 1975). The nasal sinuses are often heavily parasitized with *Nasitrema dalli* (Dailey, 1971; Dailey and Walker, 1978; Yamaguti, 1951), *Torynurus dalli* (Cowan et al., 1986; Dailey and Walker, 1978), *Stenurus minor* (Dailey and Walker, 1978; Johnston and Ridgway, 1969), or *Phararus dalli* (Dailey, 1971). *Phararus* and *Stenurus* have also been discovered in the inner ear area (Machida, 1974; Walker, 1975). The trematode *Campyla oblonga* is a common parasite of the liver and pancreas, as well as their associated ducts (Conlogue et al., 1985; Cowan et al., 1986; Dailey and Walker, 1978; Machida, 1974; Yamaguti, 1951). The stomach is sometimes infested with *Anisakis simplex* (Dailey, 1971; Machida, 1974). The nematodes *Crassicauda* and *Placentonema* commonly inhabit the blubber and muscle of the urogenital area (Conlogue et al., 1985; Ridgway, 1966; Walker, 1975).

Ectoparasites appear to be uncommon on Dall's porpoises, but Leung (1967) reported whale lice (*Neocyamus physteris*) from Japanese animals. Morejohn (1979) has reported the commensal

diatoms *Amphora lineolata*, *Trachyneis aspera*, and five forms of *Cocconeis ceticola* from various locations on the surface of Dall's porpoises from California.

The large daily food requirements of captive animals suggest a high metabolic rate (Ridgway, 1966; Walker, 1975). Throughout their range, Dall's porpoises feed mainly on epi- and meso-pelagic squids and small schooling fishes (mostly <30 cm in length). In Monterey Bay, where the species' feeding habits have been well studied, Pacific hake (*Merluccius productus*), Pacific herring (*Clupea harengus*), northern anchovy (*Engraulis mordax*), juvenile rockfish (*Sebastes*), and market squid (*Loligo opalescens*) form the major part of their diet (Loeb, 1972; Morejohn, 1979). In the northwestern North Pacific, squids (Goniatidae), and lanternfish (Myctophidae) appear to be the most important prey species (Crawford, 1981; Mizue and Yoshida, 1965; Mizue et al., 1966). Salmon (*Oncorhynchus*) is not a regular food item (Crawford, 1981; Mizue et al., 1966). Occasionally these animals take crustaceans such as decapods and euphausiids (Crawford, 1981; Morejohn, 1979).

Dall's porpoise is probably best described as an opportunistic feeder, and a large variety of prey species have been identified (Stroud et al., 1981). The deep-diving habits of Dall's porpoises have been inferred from aspects of physiology and morphology (Ridgway, 1966, 1972; Ridgway and Johnston, 1966) and from deep-water fish found in Dall's porpoise stomachs (Loeb, 1972; Morejohn, 1979; Stroud et al., 1981). These animals generally have been thought of as nocturnal feeders (Crawford, 1981; Morejohn, 1979; Stroud et al., 1981).

Dall's porpoises are taken in several fisheries, mostly in the western Pacific. Porpoises are harpooned as they ride the bow wave in a fishery off the Sanriku coast of Japan, where the meat is used for human consumption. The catch in the 1960s and 1970s generally had been <9,000/year (Kasuya, 1982; Miyazaki, 1983), but it expanded to other areas and increased to near 13,000 in 1982 and 1983 (International Whaling Commission, 1984, 1985). The Japanese-salmon-mothership fishery operates in the northwestern North Pacific Ocean and Bering Sea, mostly within the United States Fishery Conservation Zone. In the past, this fishery was much more extensive, and incidental kills of 10,000 to 20,000 were considered possible when the estimated unreported take was included (Mizue and Yoshida, 1965). In recent years, the take has decreased to an estimated 3,200 in 1985 (International Whaling Commission, 1987). Salmon research vessels also kill a number of Dall's porpoises in the western North Pacific area (Ohsumi, 1975). The Japanese land-based salmon fishery operates in the region southwest of the mothership area. There is little information available for this fishery, but the 1982 take, based on the observed take rate from the mothership fishery was estimated at about 6,100 (Jones, 1984). An extensive squid driftnet fishery by Japan, Taiwan, and Korea operates in the North Pacific, and is relatively unmonitored. The catch of *P. dalli* is unknown, but it is suspected to be substantial. The effects of these fisheries on the Dall's porpoise populations involved remain uncertain.

In the Sea of Japan and Okhotsk Sea, porpoises were exploited more heavily in the past, but at present suffer only a small incidental catch (Kasuya, 1982). There is no commercial exploitation of this species in the eastern North Pacific, but a few animals are taken incidentally to other fishing operations (Everitt, 1980; Jefferson, 1987; Loughlin et al., 1983).

Small numbers of Dall's porpoises have been live-captured in the United States (Norris and Prescott, 1961; Ridgway, 1966; Walker, 1975; Wood, 1973) and Japan (Kasuya et al., 1984). These animals do not do well in captivity, and most specimens have died during or within the first few weeks after capture.

Until recently, little work had been done looking at pollutant levels in Dall's porpoise tissues. O'Shea et al. (1980) discovered several organochlorine contaminants in the tissues of a Dall's porpoise from southern California, including particularly high concentrations of DDT. Subramanian et al. (1986) found differences in PCB and DDE concentrations of porpoises from the Bering Sea and those from the North Pacific, suggesting that they come from separate populations. PCB and DDE levels tend to be lower in females (due to parturition and lactation), but high levels in males can result in reduced testosterone levels (Subramanian et al., 1987a, 1987b).

Dall's porpoise is generally considered to be a continental-shelf and slope species, but it also inhabits deep waters more than 1,000 km from shore (Kasuya and Jones, 1984). When found near shore, Dall's porpoises tend to inhabit wide straits (Scheffer, 1949), deep open-ended channels with strong currents (Cowan, 1944), or deep

canyons (Loeb, 1972). They are frequently encountered in the deeper inshore waters of Washington, British Columbia, and Alaska (Leatherwood et al., 1982).

Water temperature seems to play a part in determining the distribution of Dall's porpoise. Kasuya (1978) sighted these animals in waters ranging from 3 to 22°C, but most sightings are in waters cooler than 17 to 18°C (Kasuya and Jones, 1984). In southern California, they seemed to move out of the area when water temperature rose above 17°C (Norris and Prescott, 1961). Water depth appears to be the other most important factor determining distribution. At least in the eastern North Pacific, *P. dalli* is found mostly in waters of 180 m and deeper (Fiscus and Niggol, 1965; Leatherwood et al., 1982; Loeb, 1972). Smith et al. (1986) present evidence that Dall's porpoise tends to be associated with high surface chlorophyll areas off the California coast.

Abundance estimates by strip and line transect methods have only recently become available, but their accuracy is questionable. An estimate of 920,000 was obtained by Bouchet (1981) for the North Pacific and Bering Sea portions of the range (excluding the Sea of Japan and Okhotsk Sea). One of the main problems with ship surveys is that the movements of the animals are often affected by the research vessels, and this results in a violation of one of the major assumptions of the analysis (Bouchet, 1981).

There appears to be some segregation by age, sex, and reproductive status in the western North Pacific (Kasuya and Jones, 1984; Wilke et al., 1953). Morejohn (1979) believed that migration patterns are strongly related to the availability of prey species. Hall (1981), however, stated that Dall's porpoises tend to have seasonal home ranges around which their movements are restricted. This species is present year-round throughout most of its range in the eastern North Pacific. Movements seem to be mostly inshore/offshore, with animals moving closer to shore in the cooler part of the year (Brown and Norris, 1956; Pike and MacAskie, 1969; Ridgway, 1966; Walker, 1975). There also appears to be a north/south component to the migration (Brownell, 1964; Leatherwood et al., 1982; Loeb, 1972). There is little indication of long north/south migrations of whole segments of the population along the North American coast, but Morejohn (1979) provided possible evidence of movements of individuals from the Bering Sea to Monterey Bay. In the western part of the range, movements appear to have a much stronger north/south component, with summers spent in the more northern portions of the range, and inshore/offshore movements seem to be less important (Kasuya, 1978, 1982; Nishiwaki, 1967; Ohsumi, 1975; Okada and Hayashi, 1951).

**BEHAVIOR.** Because of the difficulty associated with keeping *P. dalli* in captivity, and their offshore distribution, their behavior has received little study. Dall's porpoises are most commonly observed playing in the bow waves of boats, darting back and forth with jerky movements (Leatherwood et al., 1982). When fast swimming such as this, the animals throw-up a V-shaped splash and thus this type of surfacing is called rooster-tailing. Subadults appear to be the most common bow-riders, with mother-calf pairs almost never being seen bow-riding (Kasuya and Jones, 1984). Fast moving boats attract Dall's porpoises, and speeds of 26 km/h (Morejohn, 1979) or up to 32 km/h (Ridgway, 1966) have been found best for keeping these animals at the bow. *Phocoenoides* is considered to be one of the fastest swimming small cetaceans off the coast of California (Brownell, 1964; Norris and Prescott, 1961; Ridgway, 1966). They may be capable of reaching speeds of nearly 55 km/h for quick bursts (Leatherwood and Reeves, 1986).

When swimming slowly, Dall's porpoises cause little surface disturbance, and the deepened caudal peduncle appears high above the surface just before the animal submerges. This type of surfacing is called slow rolling. Speeds of slow rolling porpoises in the Johnstone Strait, British Columbia, Canada, have been reported to average about 5 km/h (Jefferson, 1987).

Two behavioral patterns have been implicated in feeding. In the first, known as "surface splash," a relatively large group of porpoises is seen slicing along the surface in a small area (G. C. Bouchet, per. comm.). There are many sharp directional changes and subsurface rolls along the longitudinal axis. Dive times seem to be short, and the porpoises are presumably feeding near the surface. The second pattern is characterized by long (2 to 4 min) dives, interspersed with series of shorter submergences (Jefferson, 1987). The animals tend to slow roll in the same area for long periods of time, and are probably feeding deeper in the water column at these times. Dive depths have not been directly measured.



Dall's porpoises are most often seen in small groups of 2 to 12, and are sometimes observed singly. Occasionally, large groups of up to several thousand are seen, and these are most likely feeding aggregations (Scheffer, 1950; Sullivan and Houck, 1979). *Truei*-type porpoises appear to form slightly larger groups than *dalli*-type (Kasuya, 1978; Kasuya and Jones, 1984; Miyazaki et al., 1984). Small groups of Dall's porpoises usually do not appear to take on any particular shape. Norris and Prescott (1961), however, reported groups of up to 100 animals swimming in single file off the coast of southern California. Large groups are often composed of smaller subgroups (Loeb, 1972).

Aerial behavior is rare in this species. Several authors have reported leaping, but it is unclear if they were referring to animals completely clearing the water, or simply to rooster-tail splashes (Lustig, 1948; Tomilin, 1967; Yocum, 1946).

Sounds produced by captive Dall's porpoises were reported by Ridgway (1966) and Evans (1973) to consist solely of low-frequency (<20 kHz) clicks. When recorded in the wild with high-frequency equipment, these animals were found to produce short (50 to 1,500  $\mu$ s), narrow-band, constant-frequency single and double pulses with peak energies between 120 and 160 kHz (Awbrey et al., 1979). These are presumably used for echolocation.

The mating system is unknown, and nothing is known of the reproductive behavior of *P. dalli*.

**GENETICS.** The chromosomes of Dall's porpoise were first described and figured by Makino (1948) and later by Kulu et al. (1971) and Kulu (1972). The diploid chromosome number is 44 (21 pairs of autosomes and one pair of sex chromosomes) and resembles the general odontocete pattern (Arnason, 1974).

No differences were found between the karyotypes of *dalli*- and *truei*-type porpoises by Yabu and Ogi (1986). The sightings of white Dall's porpoises by Joyce et al. (1982) may have been of albinos. Hain and Leatherwood (1982), however, cautioned that there are other genetic conditions which can produce anomalously white cetaceans.

**REMARKS.** The taxonomic status of the genus is not firmly settled. Some researchers still refer to *dalli*- and *truei*-types as separate species or subspecies. Most seem to accept the conclusion of Houck (1976) that they are color morphs of the same species. This is further supported by the following points: intermediate color types have been examined (Houck, 1976), mixed schools of the two types commonly are seen (Houck, 1976; Kasuya, 1978; Kuroda, 1954; Miyazaki et al., 1984), fetuses of one type have been found in mothers of the other (Newby, 1982; Wilke et al., 1953; but see also Kasuya, 1978, 1982), and the two types are genetically almost identical (Shimura and Numachi, 1987). Ongoing studies, through the cooperative U.S.-Japan research program may resolve this controversy in the near future (Jones, 1981).

Barnes (1984, 1985) has suggested that phocoenids (true porpoises) represent two separate evolutionary lines, and that these be designated as the subfamilies Phocoeninae and Phocoenoidinae. Phocoenoidinae would contain the extant species *Phocoenoides dalli* and *Australophocaena dioptrica* (= *Phocoena dioptrica*), as well as several extinct species. Barnes (1985) reported that *P. dalli* and *A. dioptrica* share several cranial and post-cranial features. In addition, they have similar color patterns and seem to possess more of an offshore distribution than other phocoenids. He suggests they may represent antitropical counterparts.

Variant spellings are *Phocaena* for *Phocoena*, *Phocaenoides* for *Phocoenoides*, and *dallii* for *dalli*. Other common names include Dall porpoise, True's porpoise, spray porpoise, white-flank porpoise, *ishi-iruka* (Japan), *rikuzen-iruka* (Japan), and *belokrylaya morskaya svin'ya* (U.S.S.R.).

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